Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content

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Equations presented in an earlier paper, expressing organic matter and nitrogen dynamics in decomposing hardwood leaf litter, are extended to predict nitrogen immobilization patterns in litters of varying initial lignin and nitrogen content. A continuum of immobilization rates coincides with the successional status of the six northern hardwood species examined, with early successional species exhibiting the fastest rates. By using data from the literature, similar trends were found for southeastern hardwoods. Patterns for important species from Douglas-fir forests of the Pacific Northwest are quite different and may reflect differences in nitrogen availability following disturbance.

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Des équations présentées dans un article antérieur décrivaient la dynamique de la matière organique et de l'azote dans la litière en décomposition de feuilles de bois durs; ces équations sont développées pour prédire les patrons d'immobilisation de l'azote dans des litières ayant diverses teneurs initiales en lignine et en azote. Une gradation des taux d'immobilisation coïncide avec la position successionnelle des six espèces de bois durs nordiques examinées; les espèces plus hâtives dans la succession ont les taux d'immobilisation les plus rapides. D'après des données tirées de la littérature, les mêmes tendances se rencontrent dans les bois durs du sud-est des Etats-Unis. Dans les forêts de Douglas taxifolié de la région Pacifique du Nord-Ouest, les patrons sont très différents, ce qui reflète peut-être des différences dans la disponibilité de l'azote après une perturbation.

[Traduit par le journal]

Introduction

The net immobilization of available, external nitrogen into decomposing plant material under both laboratory and field conditions has been well documented (Waksman and Gerretsen 1931; Richards and Norman 1931; Bocock 1964; Gosz *et al.* 1973). Much research performed early in this century attempted to determine the amount of nitrogen required to "decompose" a given residue, with the goal of optimizing the production of useable soil amendments for agriculture. Hutchinson and Richards (cited in Richards and Norman 1931) defined the "nitrogen factor" as the amount of nitrogen that could be incorporated into decomposing tissues without loss, or the amount immobilized before net mineralization begins. Research on different plant materials yielded "nitrogen factors" for each, but although biochemical quality of the substrate was indicated as important, no clear determination as to the underlying causes of the nitrogen factor was developed (Richards and Norman 1931; Norman 1931*a*, 1931*b*). Waksman and co-workers (Waksman and Tenney 1927, 1928; Waksman and Gerretsen 1931) determined that temperature, moisture, external nitrogen supply, and substrate quality all affected decomposition rate and nitrogen immobilization, but again no predictive theory was produced.

The advent of "chemical" farming apparently reduced the importance of this type of research, for although much has been learned of the nature and structure of soil organic matter (e.g., Allison 1973), relatively little research has been done recently on the decomposition of fresh agricultural wastes.

In contrast, decomposition has emerged as a very important component of the study of nonagricultural ecosystems as it represents a crucial process in the cycling of nutrients, especially nitrogen (e.g., Gosz *et al.* 1973; Bormann *et al.* 1977; Henderson *et al.* 1978). In these systems, especially forest ecosystems, which yield products without a substantial fertilizer input, management of the nutrient cycle represents an important means of maintaining productivity and a sustained yield (Aber *et al.* 1978, 1979; White 1974). Short-term effects of processes such as the net immobilization of nitrogen into decomposing material can be crucial

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during periods of rapid nutrient mobilization and loss in some ecosystems following disturbance (Bormann and Likens 1979; Vitousek *et al.* 1979). Again, nitrogen receives special attention owing to a general suboptimal availability in forests (Mitchell and Chandler 1939; Auchmoody and Filip 1973; Cole and Gessel 1965) and the ease with which it can be leached from forest soils, especially in the nitrate form. All of this makes predictive knowledge of the "nitrogen factor" or more generally the nitrogen dynamics of decaying plant material very important in the study and management of forest ecosystems.

Not surprisingly, most of the same factors identified as important in the optimal decay of agricultural residues have been found to be important for forest litter decomposition. Cromack and co-workers (Cromack 1973; Fogel and Cromack 1977) have shown that biochemical complexity as indicated by percent lignin content is inversely related to rate of decay. Meentemeyer (1978) has extended this analysis to predict geographic patterns of decay based on lignin content and actual evapotranspiration, a combination of temperature and precipitation. Melillo *et al.* (1982) have shown that decay rates in a given stand are predicted by the ratio of lignin to nitrogen in the original material.

The nitrogen dynamics (immobilization–mineralization) of leaf litter of a given species have also been shown to be predictable in that a linear relationship has been demonstrated between percent of original weight remaining and the nitrogen concentration in the litter–microbe residue (Aber and Melillo 1980). The purpose of this paper is to present a set of quantitative relationships based on this latter work which allow the determination of the total amount of nitrogen immobilized by a given type of litter and the rate at which this immobilization occurs.

The method

Figure 1 presents data for the decomposition of leaf litter from six species of deciduous trees in the northern hardwood forest type of northern New England presented in this inverse-linear format (see Melillo *et al.* (1982) for discussion of methods and Aber and Melillo (1980) for the generality of this relationship). This essentially expresses nitrogen immobilized per unit weight loss, a value termed the "nitrogen equivalent" by Richards and Norman (1931). The equations developed by Melillo *et al.* (1982) allow the quantitative determination of the rate of weight loss and the nitrogen dynamics of the process for six leaf litter types in northern hardwood forests. We will present here predictions for the amount of nitrogen immobilized per gram original weight (nitrogen factor) and per gram weight lost (nitrogen equivalent) and the percent of original weight remaining when the switch from net immobilization to net mineralization occurs.

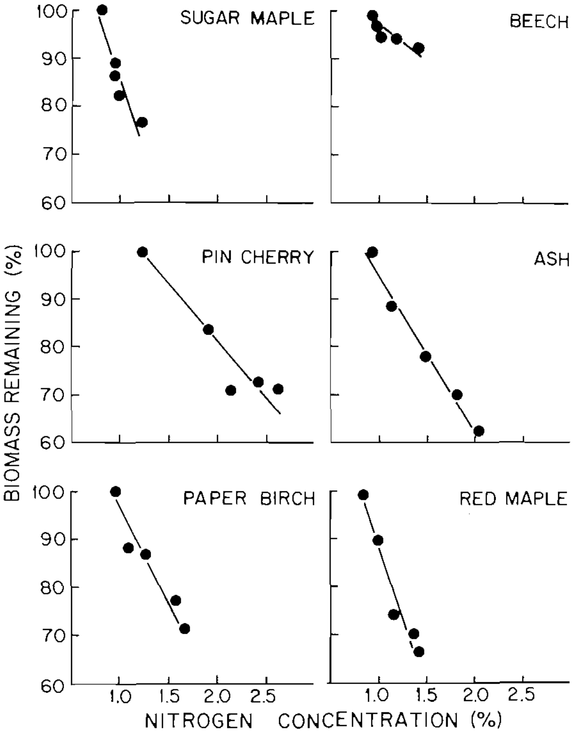

FIG. 1. Data on decomposition of leaf litter for six northern hardwood species presented in the inverse-linear format of Aber and Melillo (1980). The species are sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), pin cherry (*Prunus pensylvanica*), white ash (*Fraxinus americana*), paper birch (*Betula papyrifera*), and red maple (*Acer rubrum*). Nomenclature after Gleason and Cronquist (1963). Data from Melillo *et al.* (1982).

Figure 2 exhibits the data for white ash leaves in Fig. 1 plotted in two ways. The lower line represents the percent of original weight remaining as a function of nitrogen concentration in the residue (same as Fig. 1). In general, the equation for the line is

[1] $Y = \text{intercept} + \text{slope}(X)$

The upper line represents the percent of original nitrogen remaining, which is [1] times the current nitrogen concentration (X) divided by the original concentration (N), or

[2] $Y = (\text{intercept} + \text{slope}(X))\ (X/N)$

which can be expressed as

[3] $Y = (\text{intercept}(X/N)) + (\text{slope}(X^2/N))$

The amount of nitrogen immobilized before net mineralization begins, expressed as a fraction of total initial

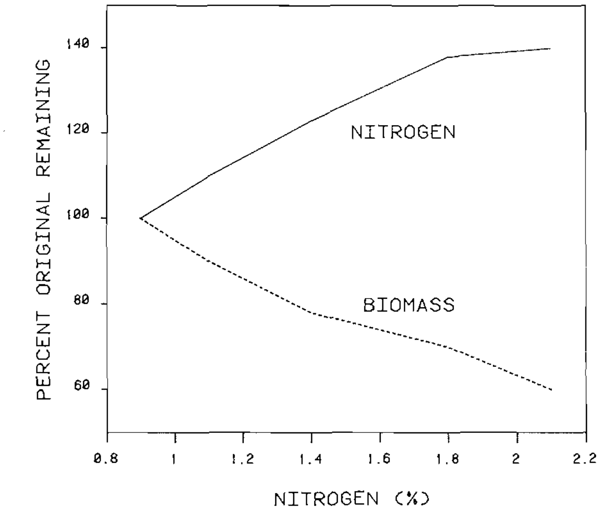

FIG. 2. Data on decomposition of leaves of white ash (*Fraxinus americana* L.). Lower line is percent original weight remaining as a function of nitrogen concentration. Upper line is percent original nitrogen remaining.

nitrogen content, is the maximum value of [3] times 1.0. This maximum will occur when the first derivative of [3] is equal to zero or

$$[4] \quad 0 = (\text{intercept}/N) + 2X(\text{slope}/N)$$

Solving for percent nitrogen we get

$$[5] \quad X_{y\,\max} = (\text{intercept}/-2(\text{slope}))$$

The percent of original weight remaining at this point is obtained by substituting [5] into [1] or

$$[6] \quad Y_{y\,\max} = \text{intercept} + \text{slope}(\text{intercept}/-\text{slope})$$

which simplifies to

$$[7] \quad Y_{y\,\max} = \text{intercept}/2$$

The "nitrogen factor" would be the amount of nitrogen at the peak in Fig. 2 minus the nitrogen in the original material or

$$[8] \quad ((Y_{y\,\max})(X_{y\,\max}) - 100\cdot(N))\ /\ 10\,000$$

(the 10 000 converts from percent values to decimal fractions), which simplifies to

$$[9] \quad (\text{intercept}^2/-4\cdot(\text{slope}) - 100\cdot(N)/1000$$

by substitution from [5] and [7].

The "nitrogen equivalent" or nitrogen fixed per unit weight loss is the total immobilization to the peak (Eq. 9) divided by the percent weight lost or (1.0 − (Eq. 7 × 0.01)). Thus, obtaining the simple linear regression in Eq. 1 for any substrate during decomposition allows direct computation of the nitrogen dynamics of the decay process. The equations developed by Melillo *et al.* (1982) allow a further quantification of this process. They present two new equations. The first,

$$[10] \quad K = 0.79 - 0.03\ (L/N)$$

(where K is percentage weight loss per year, L is percent lignin in initial material, and N is percent nitrogen in initial material) expresses the rate of weight loss as a function of the initial lignin and nitrogen concentration in the material and adds a time component to the above relationships. The data in Figs. 2 and 3 are independent of time. More importantly, Melillo *et al.* (1982) produce a regression for the slope of the relationship in Fig. 1 as a function of initial lignin concentration. This is

$$[11] \quad \text{slope} = -56.1 + 1.86(L)$$

The intercept in Eq. 1 is then

$$[12] \quad \text{intercept} = 100\cdot\ -\text{slope}(N)$$

Substituting these into Eq. 9 yields

$$[13] \quad \left(\left(\frac{(100\cdot\ -(-56.1 + 1.86(L))(N))^2}{4\cdot(-56.1 + 1.86(L))}\right) - 100\cdot(N)\right)/\ 10\,000$$

which expresses total nitrogen immobilization by any substrate as a function of its initial nitrogen and lignin content. Dividing this by 1.0 minus the percent weight remaining when immobilization ceases (Eq. 7 × 0.01) will estimate nitrogen immobilization per unit weight loss. A final expression can be obtained by multiplying this factor by the percent disappearance per year (Eq. 10), which predicts total immobilization by a litter type during the 1st year of decomposition. This is subject to the constraint that it be less than the total immobilization value.

Figure 3 presents the predictions from Eq. 13 for total immobilization (nitrogen factor) for litter of different initial lignin and nitrogen content. This shows that total immobilization increases with increasing initial lignin content and decreasing initial nitrogen. Figure 4 is drawn from Eq. 13 with values divided by (1· − (Eq. 7 × 0.01)), which expresses nitrogen immobilization per unit weight loss (nitrogen equivalent). The trends are the same as in Fig. 3, but the absolute values vary owing to differences in the percent of original weight remaining when the material switches from immobilization to mineralization. Other workers (e.g., Gosselink and Kirby 1974) have used the nitrogen immobilization per unit weight loss as a measure of increase in microbial biomass and hence an indicator of the efficiency of microbial utilization of substrate. If this truly represents efficiency, then we have the counter-intuitive result that

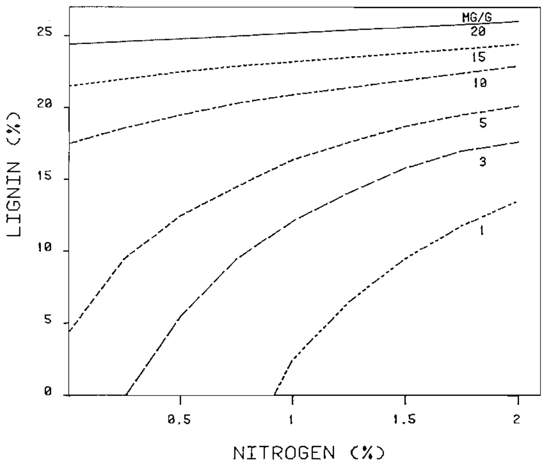

FIG. 3. Total nitrogen immobilized (miligrams) per gram litter as a function of initial lignin and nitrogen content.

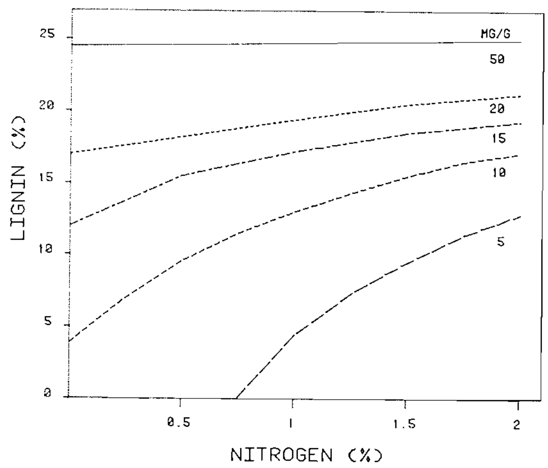

FIG. 4. Total nitrogen immobilized (milligrams) per gram weight loss during decomposition as a function of initial lignin and nitrogen content.

efficiency is directly related to initial lignin content and inversely related to initial nitrogen. An alternative hypothesis is that a lignin-rich substrate provides more material for the production of prehumic substances and that much of the retained nitrogen is in the form of protein–lignin complexes rather than in micobial protein. Thus, immobilization potential may be more a function of incomplete degradation (potential for humic formation) than speed of decomposition.

This is further substantiated in Fig. 5, which depicts percent weight loss per year and is derived from Eq. 10. The trends are the opposite of those in Figs. 3 and 4, increasing with decreasing lignin and increasing nitrogen content. The limitation of the linear regression and the range of data represented in the original study are shown in the calculation of negative decay values for the upper left corner of this figure. A wider range of materials would allow a more complete analysis. However, most deciduous leaf litter will fall within the range of positive decay rates.

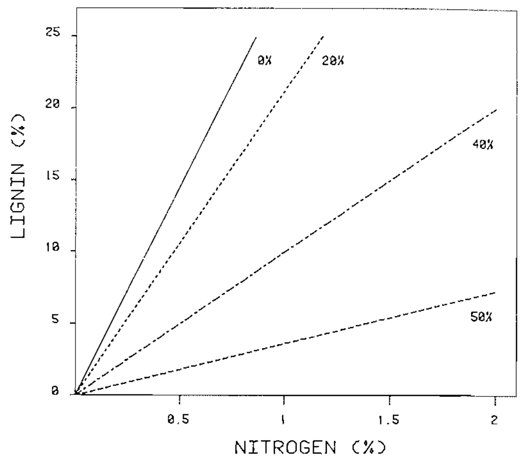

FIG. 5. Percent weight loss per year from decomposition as a function of initial lignin and nitrogen content.

Figure 6 presents net nitrogen immobilization in the 1st year of decomposition, a combination of Figs. 4 and 5, subject to the constraint that the value be less than total immobilization. The positions of our six species on this figure are also depicted. These results are especially intriguing and may begin to illustrate important mechanisms for the control of nutrient cycling by species through litter quality. They may also be interpretable in terms of the successional status of the species and the conditions under which they grow.

The highest immobilization rates (gram N immobilized per gram litter input per year) occur in litters high in both lignin and nitrogen. This is because total immobilization increases with lignin content, while rate of decay increases with nitrogen content. One could hypothesize that species adapted to high nitrogen availabilities should exhibit minimal immobilization to speed the nitrogen cycle. They should, in other words, have high nitrogen and low lignin content in their leaf litter. However, the opposite seems to be true. Secondary succession following harvest in this northern hardwood forest type generally begins with a rapid growth of pin cherry under very high nitrogen availabilities as evidenced by stream water concentrations (Marks 1974; Bormann and Likens 1979). Pin cherry production declines along with nitrogen availability through the first 10–20 years (Covington and Aber 1980). In Fig. 6, pin cherry shows the highest immobilization rate in terms of nitrogen immobilized per gram leaf litter per year. Thus, in addition to acting as an important nutrient sink following disturbance by rapid nutrient uptake (Marks and Bormann 1972; Marks 1974), pin cherry may also

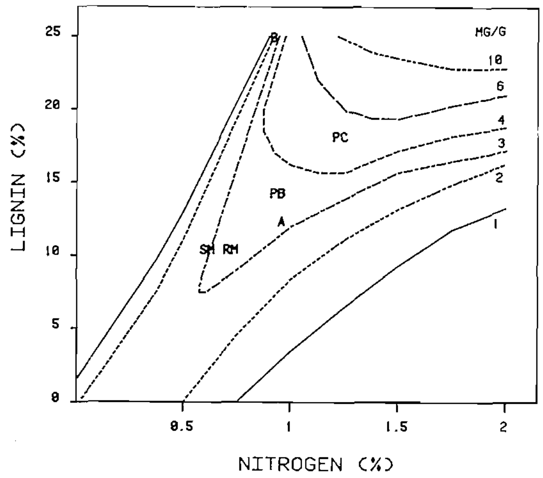

FIG. 6. Nitrogen immobilization (milligrams) per gram litter in the 1st year of decomposition as a function of initial lignin and nitrogen content. Species used in deriving equations are positioned according to chemistry of leaf litter. Species are as follows: PC, pin cherry (*Prunus pensylvanica*); PB, paper birch (*Betula papyrifera*); A, white ash (*Fraxinus americana*); RM, red maple (*Acer rubrum*); SM, sugar maple (*Acer saccharum*); B, beech (*Fagus grandifolia*). Nomenclature after Gleason and Cronquist (1963).

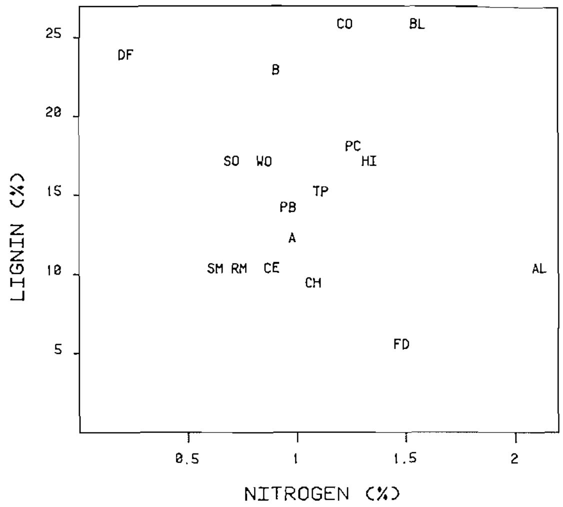

FIG. 7. Position of several species on lignin–nitrogen axes as determined by content of leaf litter. Northern hardwood species same as in Fig. 4. Additional species are as follows: southeastern hardwoods: BL, black locust (*Robinia pseudoacacia*); CO, chestnut oak (*Quercus prinus*); SO, scarlet oak (*Q. coccinea*); WO, white oak (*Q. alba*), HI, hickory (*Carya* spp.); TP, tulip poplar (*Liriodendron tulipifera*); CH, chestnut (*Castanea dentata*); FD, flowering dogwood (*Cornus florida*); Pacific Northwest: DE, Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco); CE, Ceanothus (*Ceanothus* spp.); AL, alder (*Alnus rubra* Bong.). Nomenclature after Gleason and Cronquist (1963) except where specified. Data from Cromack (1973, personal communication).

act to hold nitrogen on site by producing litter capable of immobilizing large quantities of nitrogen in the 1st year. Assuming a canopy of 2.5 t/ha of pin cherry leaves (Marks 1974), roughly 15 kg nitrogen/ha would be immobilized by 1 year's litter. This would act to hold nitrogen on site and, through rapid transformation and possibly increased humus production per gram of litter, serve to reconstruct the soil organic matter which is being oxidized at a greatly increased rate (Bormann *et al.* 1974). The remaining species have immobilization rates which vary directly with their successional status, indicating a potential relationship between success in disturbed sites and immobilization potential of leaf litter.

The rates discussed above are most important immediately after disturbance for retaining nitrogen within the system. For soil systems not recently subjected to a major disturbance, the rates of decay and total immobilization become more important in determining nitrogen dynamics. For example, beech litter will accumulate a larger standing crop of organic matter and nitrogen in the 01 horizon owing to its slow decay rate and high total immobilization. In pure stands, and depending on other site factors, this could result in the kind of nutrient stagnation cited for some far-northern forest types (Viro 1974). We might expect beech to grow better under low nitrogen conditions than some other northern hardwood species. Nitrogen would cycle more rapidly in an equilibrium forest floor derived from the more rapidly decomposing species (e.g., sugar maple).

This same pattern for changing lignin and nitrogen content of litter with succession may not hold for other types of forest ecosystems. Figure 7 places 19 species from three forest regions in the same two-dimensional lignin–nitrogen space as shown in Figs. 3–6. Two trends emerge from these data: (*1*) early successional and understory species plus symbiotic nitrogen fixers have high nitrogen concentrations; and (*2*) late successional species generally associated with poor site conditions have high lignin concentrations.

In terms of successional patterns, the species from the Pacific Northwest of the United States exhibit a sequence very different from northern hardwoods, switching from high nitrogen, low lignin litter (alder and *Ceanothus*) to low nitrogen, high lignin (Douglas-fir). This could be correlated with a generally low nitrogen availability in this forest type (Vitousek and Melillo 1979) and high "resistance" to nitrogen losses following disturbance (Vitousek *et al.* 1979). The rich litter from these early successional deciduous species may serve to increase the rate of nitrogen cycling, in addition to the direct effects of these species through symbiotic nitrogen fixation. This is in contrast with the high potential for immobilization and humus formation in pin cherry which grows in systems where nitrogen availability is very high following disturbance.

In southeastern United States forest ecosystems, successional patterns may be similar to northern hardwoods, with black locust exhibiting even higher nitrogen and lignin contents than pin cherry. The high content of lignin in this symbiotic nitrogen fixer is in marked contrast with the values for alder and *Ceanothus* spp. White oak and scarlet oak have intermediate lignin and nitrogen values and chestnut oak may represent the poor-site dominant similar to beech. Chestnut may have been the rich-site equivalent of sugar maple before its elimination by the chestnut blight. If so, the loss of this species as a major component of southeastern ecosystems may have had greater effects on system function than has been predicted by computer models of competitive interactions between species (Shugart and West 1977).

In summary, we have shown that the lignin and nitrogen content of litter can cause large changes in the rate and nitrogen dynamics of decomposition. Different species exhibit a wide range of lignin and nitrogen concentrations, which could lead to very different rates of nitrogen cycling. Thus, the biochemical quality of litter may be related to a species' nitrogen requirement and successional status and may be a crucial component of both interspecific plant competition and overall ecosystem function.

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